

Floristics of the South American Páramo Moss Flora

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Abstract. The South American paramos appeared in Pliocene times and persist to the present day. The moss flora of this habitat consists of an estimated 400 species that comprise 8 floristic groups. In Venezuela these groups and their percent representation are as follows: neotropical 37%, Andean 26%, cosmopolitan 18%, Andean-African 8%, neotropical-Asiatic 3%, neotropical-Australasian 2%, temperate Southern Hemisphere 2% and northern boreal-temperate 2%. Acrocarpous taxa outnumber pleurocarps by nearly 3:1. The neotropical and Andean floristic stocks likely were present prior to late Pliocene orogenies that elevated the cordillera above climatic timberlines. These species may have existed in open, marshy areas (paramillos) or may have evolved from cloud forest ancestors. Taxa of northern boreal-temperate affinities, including those with Asiatic distributions, probably arrived in the paramos during the Pleistocene, a period which may also have seen the establishment in the Northern Andes of some cosmopolitan elements. Species with temperate Southern Hemisphere and Australasian affinities likely spread first to austral South America thence migrated northward during a cool, moist interval sometime over the past 2.5-3 million years or may have become established in the paramos as a result of long-distance dispersal.

Reconstructing a floristic history for the páramo mosses of South America requires addressing a number of questions. When did the páramo life zone appear and supposedly become available to colonizing species? Here we can be rather precise. From the pioneering work of Thomas van der Hammen and his coworkers (cf. van der Hammen 1974; van der Hammen & Cleef 1983, 1986), it is clear an upper elevational timberline did not develop in the Northern Andes before late Pliocene time (ca. 2-4 million years B.P.). The development of a páramo system is revealed by a study of pollen deposited in lake sediments and is signaled by a sharp rise in the frequency of pollen types assignable to the Poaceae and Asteraceae and a concomitant decrease in

pollen of Andean forest taxa. The establishment of this chronology for the páramo habitat has important implications for floristic reconstructions since it sets the time frame within which the earliest colonists must have arrived. It does not establish; however, where the páramo moss species (or their antecedents) were in the period prior to the development of a páramo system (although we can speculate on this point) nor does it tell us exactly how old a particular páramo species is.

What are the broad outlines of the páramo moss flora? Here again, we are in a position to give a fairly detailed answer. Accelerated field work over the past 25 years in the principal páramo countries of Ecuador, Colombia and Venezuela has

brought into herbaria thousands of fresh collections a majority of which have been identified at least to the level of genus. Much of this identification work remains to be published, but, in general terms, we can observe that the páramo moss flora is distributed among approximately 45 families, 120-140 genera and approximately 400 species. The great majority of the species belong to acrocarpous groups. Acrocarpy appears to be favored over pleurocarpy in exposed environments as a check of some selected floras confirms. For the following floras an acrocarp/pleurocarp ratio is given (numbers represent percent of total flora) along with the references consulted: Alaskan tundra 75/25 (Steere 1978), alpine zone of Mexico 93/7 (Delgadillo 1971, 1979, 1982, 1984, 1986, 1987), páramos of Costa Rica 67/33 (Bowers 1974), páramos of Venezuela 72/28 (Griffin, this paper), Antarctica 81/19 (Robinson 1972). Vitt (1979) reported a preponderance of acrocarpous taxa in polar floras of both hemispheres and in the temperate floras of the Southern Hemisphere with a shift toward more pleurocarpous species in tropical floras and those of temperate latitudes in the Northern Hemisphere. While valid as generalizations, these trends can change for more localized regions or habitats. I believe the more universal correlative is degree of exposure (i.e., likelihood of periodic drying), regardless of which hemisphere is examined. Forested areas tend to support pleurocarp-rich floras, as seen in the case of the Great Lakes area 53/47 (Crum 1976) or Mont Bokor, Cambodia 41/59 (Tixier 1979), whereas relatively treeless areas appear to favor acrocarps.

The high elevation moss flora of Venezuela has been studied in some detail, and it can be used as a model for discussing floristic groups throughout the Andean páramo life zone. It should be recognized; however, that the Venezuelan páramos are comparatively drier than those found in

Colombia or Ecuador, a distinction that will undoubtedly be reflected in the particular percent representation of the following floristic groups in those countries.

The diverse nature of the páramo flora in Venezuela can be appreciated from the fact that while this habitat occupies 4,100 square kilometers (Jahn 1931), it represents less than 1% of the Venezuelan national territory yet supports 39% of the total known moss flora for the country. There are approximately 700 species of Musci in Venezuela (Griffin 1975, 1977a, 1977b, 1979; Griffin, Lopez & Ruiz-Teran 1973; Pursell 1973) of which 272 (Griffin, this paper) have been found above timberline in the Venezuelan Andes.

The páramo moss flora of Venezuela can be partitioned into 8 floristic groupings. These are (with percent representation): neotropical (37%), Andean (26%), cosmopolitan (18%), Andean-African (8%), neotropical-Asiatic (3%), neotropical-Australasian (2%), temperate Southern Hemisphere (2%) and northern temperate/boreal (2%).

Neotropical Element

This component of the páramo flora consists of those taxa of wide distribution in the neotropics. Few, if any, are restricted to habitats above timberline and likely were present before the appearance of a páramo life zone. These species evidently were preadapted to surviving under the more stressful conditions of the páramo environment. Included in this element are species found in forests, forest clearings and savannahs. Some representatives of this group are: *Sphagnum meridense* (Hampe) C. Müll., *S. sparsum* Hampe, *Fissidens repandus* Wils., *Ditrichum rufescens* (Hampe) Broth., *Campylopus heterostachys* (Hampe) Jaeg., *Pilopogon gracilis* (Hook.) Brid., *Bryoerythrophyl-lum jamesonii* (Tayl.) Crum, *Entosthodon jamesonii* (Tayl.) Mitt., *Bryum*

beyrichianum (Hornsch.) C. Müll., *Bryum grandifolium* (Tayl.) C. Müll., *Pohlia papillosa* (C. Müll. ex Jaeg.) Broth., *Bartramia potosica* Mont., *Ptychomitrium chimborazense* (Mitt.) Jaeg., *Macromitrium guatemalense* C. Müll., *Orthotrichum pycnophyllum* Schimp., *Zygodon pichinchensis* (Tayl.) Mitt., *Lepyrodium tomentosus* (Hook.) Mitt., *Porotrichum longirostre* (Hook.) Mitt., *Daltonia gracilis* Mitt., *Rigodium toxarion* (Schwaegr.) Jaeg., *Brachythecium stereopoma* (Spr. ex Mitt.) Jaeg., *Plagiothecium conostegium* Herz., *Catagonium brevicaudatum* C. Müll. ex Broth., *Aptychella prolifera* (Broth.) Herz., *Sematophyllum swartzii* (Schwaegr.) Welch & Crum and *Hypnum amabile* (Mitt.) Hampe.

Andean Element

This is a montane component which, like the neotropical element, most likely was in place before the appearance of the páramo habitat. As such, most of these species occur in Andean forests as well as páramos. Some typical members of the group are: *Pleuridium andinum* Herz., *Campylopus argyrocaulon* (C.M.) Broth., *Campylopus cucullatifolius* Herz., *Kingiobryum paramicola* H. Robins., *Oreoweisia tunariensis* Herz., *Aloinella venezuelana* Griffin, *Leptodontium erythroneuron* Herz., *L. stellaticuspis* Bartr., *Racomitrium steerei* Griffin, *Splachnum weberbaueri* Reimers, *Tayloria rubicaule* A. Kop., *Acidodontium heteroneuron* (Mitt.) Broth., *Schizymenium pseudopohlia* Shaw, *Bartramia humilis* Mitt., *Macromitrium trachypodium* Mitt., *Orthotrichum grande* Lewinsky, *Racopilum intermedium* Hampe, *Braunia laxifolia* Herz., *Papillaria penicillata* (Dozy & Molk.) Broth., *Neckeradelphus obtusifolius* (Tayl.) Steere, *Daltonia latolimbata* Broth., *Callicostellopsis meridensis* (C. Müll.) Broth., *Hookeriopsis steerei* Griffin, *Brachythecium herzogii* Broth., *Pogonatum andinum* (Hampe) Mitt. and *Polyti-*

chadelphus ciliatus (Hook. f. & Wils.) Mitt.

Cosmopolitan Element

The cosmopolitan element of the páramo moss flora contains a diverse assortment of species which, while sharing multicontinental distributions, are otherwise very different. The time of their appearance in the páramos and the migratory tract by which they arrived are virtually impossible to ascertain. Some were surely present prior to the development of the páramos, others may have arrived by long-distance dispersal while still others undoubtedly came in stages utilizing stepping stone habitats that must have been available during the period of the Pleistocene. Included in this group are species which produce sporophytes readily and others for which only gametophytes are known. Some representatives are: *Sphagnum magellanicum* Brid., *Andreaea rupestris* Hedw., *Fissidens asplenioides* Hedw., *Ceratodon stenocarpus* BSG, *Distichium capillaceum* (Hedw.) BSG, *Campylopus flexuosus* (Hedw.) Brid., *Anoetangium aestivum* (Hedw.) Mitt., *Didymodon vinealis* (Brid.) Zander, *Grimmia ovalis* (Hedw.) Lindb., *Funaria hygrometrica* Hedw. var. *calvescens* (Schwaegr.) Mont., *Anomobryum filiforme* (Dicks.) Husn., *Bryum argenteum* Hedw., *Bryum billardieri* Schwaegr., *Aulacomnium palustre* (Hedw.) Schwaegr., *Philonotis hastata* (Dub.) Wijk & Marg., *Orthotrichum rupestre* Schwaegr., *Hedwigia ciliata* (Hedw.) P.-Beauv., *Calliergon sarmentosum* (Wahl.) Kindb., *Pleurozium schreberi* (Brid.) Mitt., *Hypnum cupressiforme* Hedw. var. *lacunosum* Brid. and *Polytrichum juniperinum* Hedw.

Andean-African Element

This suite of species includes those disjunct between the Andes (and, in some cases, other neotropical montane habitats) and

Africa. There is reason to believe that these taxa do not represent a single floristic element in the sense of sharing the same migrational history. This can be surmised by considering the details of their distribution, especially in Africa. A species like *Brachymitrion jamesonii* Tayl., known from several localities in the Andes, but in Africa apparently restricted to Mt. Cameroon, may be presumed to have had a different floristic history from that of *Aongstroemia julacea* (Hook.) Mitt., a high elevation species in the neotropics, but found in several areas of Southern Africa and on nearby Indian Ocean islands at relatively moderate elevations. However, until more information is available concerning the history, complete distribution and ecology of these species, they will continue to be treated as a single, if heterogeneous, floristic unit. Specific examples are: *Aongstroemia julacea* (Hook.) Mitt., *Campylopus chrismarii* (C. Müll.) Mitt., *Campylopus jamesonii* (Hook.) Jaeg., *Leptodontium capituligerum* C. Müll., *L. luteum* (Tayl.) Mitt., *Streptopogon calymperes* C. Müll. ex Geh., *Brachymitrion jamesonii* Tayl., *Bryum ellipsifolium* C. Müll., *Schizymenium campylocarpum* (Hook. & Arn.) Shaw, *Diplostichum longirostre* (Brid.) Mitt., *Breutelia tomentosa* (Brid.) Jaeg., *Prionodon densus* (Hedw.) C. Müll., *Zelometeorium patulum* (Hedw.) Manuel, *Palamocladium leskeoides* (Hook.) Britt. and *Pogonatum oligodes* (C. Müll.) Mitt.

Neotropical-Asiatic Element

This relatively minor component of the páramo moss flora encompasses those species occurring on the Asian continent (and/or offshore islands) and in the neotropics. In the New World part of their range they are found typically at mid to upper elevations. Among some who have examined certain vascular plant species with similar amphi-North Pacific distributions there seems to be a presumption favoring an Asian, or, at least, Old World

origin for these elements with subsequent migration to the New World (cf. Hong 1983; Sharp 1966, 1972). This presumption may or may not be valid for mosses, but, to the extent that this scenario is plausible, it could be suggested that the Asian component of the present day páramo flora migrated first to North America, likely prior to the Pliocene when climatic conditions would have been more amenable to the migration of species requiring cool, moist environments and then, in stages, southward onto the South American mainland. As in the case of some vascular plant species, several of the Musci with this distribution pattern have disappeared from the north temperate part of their New World range. Conceivably, although less likely, a few Asian-neotropical disjunctions may have come about by long-distance dispersal. Almost all of the taxa included in this group have retained their taxonomic uniformity throughout their range, both Old World and New World. One exception is *Rozea* which has developed different but related species on the two continents (Buck and Crum 1976). The relevant taxa are: *Aongstroemia orientalis* Mitt., *Bryoerythrophyllum recurvum* (Griff.) Saito, *Plagiomnium rhynchophorum* (Hook.) T. Kop., *Steerecleus serrulatus* (Hedw.) H. Robins., *Pseudotaxiphyllum distichaceum* (Mitt.) Iwats., *Pylaisiella falcata* (BSG) Ando and *Rozea* spp.

Neotropical-Australasian Element

This disjunct floristic group includes those species with an amphi-South Pacific distribution, occurring in Southeastern Australia/New Zealand and in the Andes of South America. Such disjunctions may be artifacts of plate separation or of long-distance transport of viable propagules. If continental drift was a factor, then we are obliged to either assign an age of over 100 million years to the species involved or presume that the modern disjuncts were derived from ancestral stock, but since the

species discussed here have not diverged sufficiently in the two disjunct parts of their range to be distinguishable taxonomically, in spite of the considerable time elapsed since plate separation, it seems more attractive to posit long-distance transport of spores as the operative agent. Recent laboratory experiments on spore viability under various conditions of storage (cf. van Zanten 1978, 1983, 1984) tend to support the hypothesis that the spores of some high latitude moss species of the Southern Hemisphere could survive transport across oceanic distances. The species of interest in the present context are: *Andreaea nitida* Hook. f. & Wils., *Fissidens rigidulus* Hook. f. & Wils., *Dicranella cardotii* (R. Brown ter.) Dix., *D. hookeri* (C. Müll.) Card. and *Entosthodon acaulis* (Hampe) Fife.

Temperate Southern Hemisphere Element

The temperate Southern Hemisphere element of the páramo flora represents a group with highly interrupted ranges at high austral latitudes. This assemblage has been called the antipodal element by some authors. Species with this type of distribution tend to occur on one or more of the subantarctic islands, on Tasmania and the extreme Southeastern corner of mainland Australia and in the Patagonia-Fuegian area of South America. Individual species may be absent from one or more of these isolated stations, but there is a certain continuity to the overall ranges of all members of the group. If hepatics are considered along with Musci, the number of these disjuncts in the Northern Andes exceeds 30 species (Griffin, Gradstein & Aguirre 1982). The Northern Andes represent, for many, the extreme northern limit of their present range, and in this area they tend to be confined to high elevation Andean forests and páramos, the life zones with the most antipodal-like climate anywhere in the neotropics. The number of these disjuncts is sharply reduced in the

Venezuelan páramos, most probably as a consequence of the relative dryness of the páramo life zone in Venezuela compared with that of Colombia or Ecuador. For Venezuela the species to be noted include: *Blindia magellanica* Schimp. in C. Müll., *Entosthodon laxus* (Wils. in Hook. f.) Mitt., *Bryum andicola* Hook. in Kunth, *Conostomum pentastichum* (Brid.) Lindb., *Amphidium tortuosum* (Hornsch.) H. Robins. and *Rhacocarpus purpurascens* (Brid.) Par.

Northern Temperate/Boreal Element

The moss species belonging to this element have wide distributions at temperate and/or boreal latitudes in the Northern Hemisphere. They show diminished abundance and lower frequency of occurrence southward. At low latitudes they are restricted to high elevation habitats. A few of these species have penetrated the Old World tropics and all are found in the South American páramos.

The most likely time for the southward extension of these northern species would have been during one or more Pleistocene glacial maxima. During these periods there was a boreal-like climate as far south as Northern Mexico and the Gulf coast of the United States. In addition, the receiving area in the Northern Andes was much enlarged, expanding the total potential area in which a colonizing population could become established. Included in this element are: *Philonotis cernua* (Wils.) Griffin & Buck, *Meesia triquetra* (L.) Aongstr., *Rhytidium rugosum* (Hedw.) Lindb., *Calliergon trifarium* (Web. & Mohr.) Kindb. and *Scorpidium scorpioides* (Hedw.) Limpr.

Discussion

From the standpoint of floristic diversity, the South American páramos are exceptionally rich, rivalled, perhaps, only by upper elevation cloud forests. This

high level of diversity can be traced to a number of factors. One of these, undoubtedly, is the complexity of páramo microenvironments. Available substrates vary from open, dry mineral soils to waterlogged peats, streams and lakes, from shaded gallery forests to dry, exposed boulders. Atmospheric humidity remains relatively high all year long. In addition, the proximity downslope of the diverse Andean forest flora provided historically an extremely rich source of potential páramo colonists as local orogenies elevated the mountain summits above timberline. An additional opportunity for increasing taxonomic breadth in the páramo flora occurred during the Pleistocene glaciation which in the Andes saw the same 4 advances and retreats as experienced at high latitudes. Van der Hammen (1974) has estimated that Andean vegetation belts moved downslope by as much as 1200-1500 meters during the last (Wisconsin) glacial. The consequent areal expansion of the páramo life zone would have been significant, permitting floristic exchanges and direct migrations between what are presently isolated páramo regions. Further, the proximity of north-temperate and boreal elements and, plausibly, of antipodal taxa to the much increased páramo area would have greatly facilitated the successful establishment of species that are considered today to represent major disjuncts.

More resistant to facile explanation is the presence in the current páramo flora of elements with African and Australasian affinities. Possible historical reconstructions appear limited to two categories, i.e., invoking continental drift or visualizing long-distance transport of viable propagules. In view of the relative taxonomic uniformity of the species belonging to these disjunct groups and in consideration of the antiquity of major plate movements, long-distance transport seems the more attractive explanation.

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